

# ASHICAULIS, A NEW GENUS FOR SOME SPECIES OF MILLEROCAULIS (OSMUNDACEAE)

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## ABSTRACT

*Millerocaulis* Erasmus ex Tidwell was established as a new genus for Miller's "*Osmundacaulis herbstii* group." *Australosmunda* Hill, Forsyth & Green was proposed subsequently for osmundaceous stems anatomically similar to *Millerocaulis*, but without leaf gaps. However, a few species of *Millerocaulis*, including its type, *M. dunlopii*, lack or have occasional leaf gaps. Therefore, *Australosmunda* is placed in the synonymy of *Millerocaulis*. *Millerocaulis* is emended to include those osmundaceous species without or having only an occasional leaf gap. Under the new arrangement, *Millerocaulis* includes four species *M. dunlopii*, *M. indica*, *M. indentata*, and *M. chubutensis*. A new genus, *Ashicaulis*, is proposed for species formerly in *Millerocaulis* having numerous leaf gaps. It contains 22 species, all of which are recognized nomenclaturally by new combinations.

## RESUMEN

*Millerocaulis* Erasmus ex Tidwell se estableció como un nuevo género para el grupo de Miller "*Osmundacaulis herbstii*". Se propuso por ello *Australosmunda* Hill, Forsyth & Green para los tallos osmundáceos anatómicamente similares a *Millerocaulis*, pero sin lagunas foliares. Sin embargo, unas pocas especies de *Millerocaulis*, incluyendo su tipo, *M. dunlopii*, carecen de o tienen ocasionalmente lagunas foliares. Por ello, *Australosmunda* se pasa a la sinonimia de *Millerocaulis*. Se enmienda *Millerocaulis* para incluir aquellas especies osmundáceas que no tienen laguna foliar o que la tienen sólo ocasionalmente. En la clasificación nueva, *Millerocaulis* incluye cuatro especies *M. dunlopii*, *M. indica*, *M. indentata*, y *M. chubutensis*. Se propone un género nuevo, *Ashicaulis*, para las especies con numerosas lagunas foliares que se incluían anteriormente en *Millerocaulis*. Contiene 22 especies que se reconocen nomenclaturalmente con nuevas combinaciones.

## INTRODUCTION

The genus *Millerocaulis* was established as a new taxon based upon the informal "*Osmundacaulis herbstii* group" that was originally discussed by Miller (1967). The "*Osmundacaulis herbstii* group" was ineffectively published (Art. 29) as a new genus *Millerocaulis* by Erasmus in his unpublished doctoral dissertation (1978). Herbst (1981:37) accepted Erasmus' *Millerocaulis* but failed to validate it with a description (Art. 32.1)" (Tidwell 1986:402). *Millerocaulis* was validated by Tidwell (1986).

*Australosmunda* was proposed for osmundaceous stems similar to *Millerocaulis*, but without leaf gaps (Hill et al. 1989; Fig. 1A). However, there are a few species in *Millerocaulis*, including its type, *M. dunlopii* (Kidston and Gwynne-Vaughan



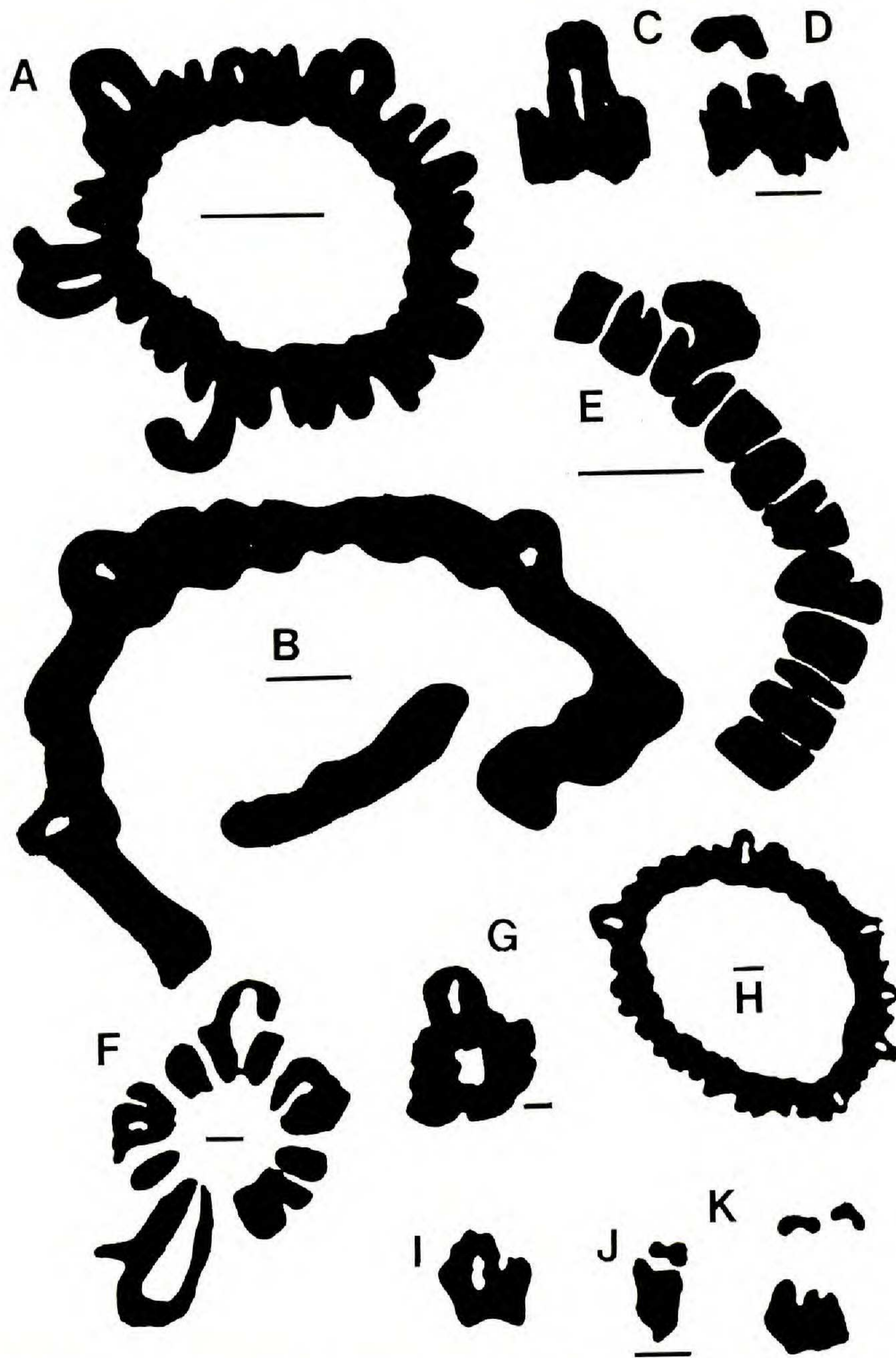


FIG. 1. Xylem cylinders and part of xylem cylinders of four species of *Millerocaulis* and two species of *Ashbicaulis* gen. nov. A. *Millerocaulis indentata* (*Australosmunda indentata*), illustrating lack of leaf gaps. B, C, D. *Millerocaulis dunlopii* B, Part of continuous xylem cylinder, C, D, stages of leaf trace formation and departure. E. *Ashbicaulis herbstii* and F. *Ashbicaulis wadei* showing many leaf gaps in their xylem cylinders. G. *Millerocaulis indica* with continuous xylem cylinder and forming leaf trace. H, I, J, K, *Millerocaulis chubutensis*, H. xylem cylinder without leaf gaps, I, J, K, leaf trace formation and departure without leaving gaps. (Bars = 1mm). (A. Drawn from holotype of *Australosmunda* (= *M.*) *indentata*, Hill et al. 1989; B, C, D, Drawn from holotype of *M. dunlopii*, Kidston & Gwynne-Vaughan 1907; E. Redrawn from Archangelsky & de la Sota 1963; F. Drawn from holotype of *Ashbicaulis wadei*, Tidwell & Rushforth 1968; G. Redrawn from Sharma 1973; H. Drawn from holotype of *M. chubutensis*, Herbst 1977, I, J, K. Redrawn from Herbst 1977).



1907; Figs. 1B, C, D), that also lack or have an occasional leaf gap. Since the type of *Millerocaulis* essentially lacks leaf gaps, *Australosmunda* is placed in the synonymy of *Millerocaulis*, and *Millerocaulis* is restricted to fossil osmundaceous axes lacking or having very rare or only an occasional ill-defined leaf gap. *Ashicaulis* is proposed for those species formerly in *Millerocaulis* that have numerous definite leaf gaps (Figs. 1E, F).

## TAXONOMY

**Millerocaulis** Erasmus ex Tidwell emend. Tidwell

Fossil osmundaceous rhizomes or arborescent axes containing stem or branching stems surrounded by a mantle of leaf bases and roots. Stele an ectophloic siphonostele, with xylem cylinder usually continuous, generally 3–15, sometimes up to 20, tracheids thick radially, with leaf gaps either totally lacking, incomplete, or very rare. Incomplete leaf gaps extending up to three-quarters through the metaxylem cylinder. Leaf trace separating from the xylem cylinder with only one protoxylem cluster and often, but not always, lacking axillary sclerenchyma. Sclerotic outer cortex of stem usually much wider than parenchymatous inner cortex. Petiole bases stipulate, and adventitious roots arising either singly or in pairs.

TYPE: *M. dunlopii* (Kidston & Gwynne-Vaughan) Tidwell (Basionym: *Osmundites dunlopii* Kidston & Gwynne-Vaughan “*dunlopi*”).

**Millerocaulis chubutensis** (Herbst) Tidwell, comb. nov. BASIONYM: *Osmundacaulis chubutensis* Herbst, *Facena* 1:25. 1977.

**Millerocaulis dunlopii** (Kidston & Gwynne-Vaughan) Tidwell, comb. nov. BASIONYM: *Osmundites dunlopii* Kidston & Gwynne-Vaughan, *Trans. Roy. Soc. Edinburgh* 45:759. 1907 (“*dunlopi*”). *Osmundacaulis dunlopii* (Kidston & Gwynne-Vaughan) Miller, *Contr. Mus. Paleo. Univ. Michigan* [21:146. 1967 (“*dunlopi*”), nom. invalid. under Art. 33.2 — no page reference to basionym] 23:135. 1971. *Osmundites aucklandicus* Marshall, *Trans. & Proc. New Zealand Inst.* 56:210. 1924.

**Millerocaulis indentata** (Hill, Forsyth & Green) Tidwell, comb. nov. BASIONYM: *Australosmunda indentata* Hill, Forsyth & Green, *Palaeontology* 32:292. 1989.

**Millerocaulis indica** (Sharma) Tidwell, comb. nov. BASIONYM: *Osmundacaulis indica* Sharma, *Palaeontographica* 140B:157. 1973.

**Ashicaulis** Tidwell, gen. nov.

Fossil osmundaceous rhizomes, rarely arborescent axes, containing stem or branching stems surrounded by a mantle of leaf bases and roots. Stele an ectophloic-dictyoxyllic-siphonostele (Miller 1971), with a xylem cylinder up to 20 tracheids thick, with many definite leaf gaps. Leaf trace separating from the xylem cylinder with only one protoxylem cluster and often, but not always, lacking axillary sclerenchyma. Commonly, the outer sclerenchymatous cortex is wider than the parenchymatous inner, rarely the same width. Petiole bases stipular and adventitious roots arising either singly or in pairs.



TYPE: *Ashicaulis herbstii* (Archangelsky & de la Sota) Tidwell (*Osmundites herbstii* Archangelsky & de la Sota).

The generic name honors my good friend and colleague Professor Sidney R. Ash of Weber State University of Ogden, Utah, in recognition of his numerous significant contributions to paleobotany. The list of species assigned to *Ashicaulis* and their synonyms are as follows:

- Ashicaulis amajolensis** (Sharma) Tidwell, comb. nov. BASIONYM: *Osmundacaulis amajolensis* Sharma, *Palaeontographica* 140B:156. 1973. *Millerocaulis amajolensis* (Sharma) Tidwell, *Sida* 11:402. 1987.
- Ashicaulis beardmorensis** (Schopf) Tidwell, comb. nov. BASIONYM: *Osmundacaulis beardmorensis* Schopf, *Can. J. Bot.* 56:3034. 1978. *Millerocaulis beardmorensis* (Schopf) Tidwell, *Sida* 11:402. 1987.
- Ashicaulis broganii** (Tidwell, Munzing & Banks) Tidwell, comb. nov. BASIONYM: *Millerocaulis broganii* Tidwell, Munzing & Banks, *Palaeontographica* 223B:98. 1991.
- Ashicaulis estipularis** (Sharma, Bohra & Singh) Tidwell, comb. nov. BASIONYM: *Osmundacaulis estipularis* Sharma, Bohra & Singh, *Phytomorphology* 8:61. 1979 ("estipulare"). *Millerocaulis estipularis* (Sharma, Bohra & Singh) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis gibbiana** (Kidston & Gwynne-Vaughan) Tidwell, comb. nov. BASIONYM: *Osmundites gibbiana* Kidston & Gwynne-Vaughan, *Trans. Roy. Soc. Edinburgh* 45:763. 1907. *Osmundacaulis gibbiana* (Kidston & Gwynne-Vaughan) Miller, *Contr. Mus. Paleontol. Univ. Michigan* [21:146. 1967, nom. invalid. under Art. 33.2 — no page reference to basionym] 23:136. 1971. *Millerocaulis gibbiana* (Kidston & Gwynne-Vaughan) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis guptai** (Sharma) Tidwell, comb. nov. BASIONYM: *Osmundacaulis guptai* Sharma, *Palaeontographica* 140B:154. 1973. *Millerocaulis guptai* (Sharma) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis hebeiensis** (Wang) Tidwell, comb. nov. BASIONYM: *Osmundacaulis hebeiensis* Wang, *Rev. Palaeobot. Palynol.* 39:93. 1983. *Millerocaulis hebeiensis* (Wang) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis herbstii** (Archangelsky & de la Sota) Tidwell, comb. nov. BASIONYM: *Osmundites herbstii* Archangelsky & de la Sota, *Ameghiniana* 3:135. 1963. *Osmundacaulis herbstii* (Archangelsky & de la Sota) Miller, *Contr. Mus. Paleontol. Univ. Michigan* (21:146. 1967, nom. invalid. under Art. 33.2 — no page reference to basionym) 23:134. 1971. *Millerocaulis herbstii* (Archangelsky & de la Sota) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis johnstonii** (Tidwell, Munzing & Banks) Tidwell, comb. nov. BASIONYM: *Millerocaulis johnstonii* Tidwell, Munzing & Banks, *Palaeontographica* 223B:94. 1991.
- Ashicaulis kidstonii** (Stopes) Tidwell, comb. nov. BASIONYM: *Osmundites kidstonii* Stopes, *Ann. Bot.* 35:55. 1921 ("kidstoni"). *Osmundacaulis kidstonii* (Stopes) Miller, *Contr. Mus. Paleontol. Univ. Michigan* (21:146. 1967 ("kidstoni"), nom. invalid. under Art. 33.2 — no page reference to basionym) 23:136. 1971. *Millerocaulis kidstonii* (Stopes) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis kolbei** (Seward) Tidwell, comb. nov. BASIONYM: *Osmundites kolbei* Seward, *Geol. Mag., NS.* 4:482. 1907. *Osmundacaulis kolbei* (Seward) Miller, *Contr. Mus. Paleontol. Univ. Michigan* (21:146. 1967, nom. invalid. under Art. 33.2 — no page reference to basionym) 23:136. 1971. *Millerocaulis kolbei* (Seward) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis liaoningensis** (Wu & Shao-lin) Tidwell, comb. nov. BASIONYM: *Millerocaulis liaoningensis* Wu & Shao-lin, *Acta Palaeontol. Sinica* 30:717. 1991.



- Ashicaulis patagonica*** (Archangelsky & de la Sota) Tidwell, comb. nov. BASIONYM: *Osmundites patagonica* Archangelsky & de la Sota, *Ameghiniana* 2:153. 1962. *Osmundacaulis patagonica* (Archangelsky & de la Sota) Miller, *Contr. Mus. Paleotol. Univ. Michigan* [21:146. 1967, nom. invalid. under Art. 33.2 — no page reference to basionym] 23:136. 1971. *Millerocaulis patagonica* (Archangelsky & de la Sota) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis rajmahalensis*** (Gupta) Tidwell, comb. nov. BASIONYM: *Osmundites rajmahalensis* Gupta, *Proc. Ind. Sci. Congr. Varanasi* 55:428. 1968. *Osmundites rajmahalensis* Gupta, *Palaeontographica* 130B:174. 1970. *Osmundacaulis rajmahalensis* (Gupta) Sharma, *Palaeontographica* 140B:152. 1973. *Millerocaulis rajmahalensis* (Gupta) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis richmondii*** (Tidwell) Tidwell, comb. nov. BASIONYM: *Millerocaulis richmondii* Tidwell, *Pap. & Proc. Roy. Soc. Tasmania* 126:1–2. 1992.
- Ashicaulis sahnii*** (Mittre) Tidwell, comb. nov. BASIONYM: *Osmundites sahnii* Mittre, *Paleobotanist* 4:113. 1955. *Osmundacaulis sahnii* (Mittre) Miller, *Contr. Mus. Paleontol. Univ. Michigan* [21:146. 1967, nom. invalid. under Art. 33.2 — no page reference to basionym] 23:135. 1971. *Millerocaulis sahnii* (Mittre) Tidwell, *Sida* 11:403. 1987.
- Ashicaulis santaecrusis*** (Herbst) Tidwell, comb. nov. BASIONYM: *Osmundacaulis santaecrusis* Herbst, *Facena* 1:21. 1977.
- Ashicaulis spinksii*** (Tidwell, Munzing & Banks) Tidwell, comb. nov. BASIONYM: *Millerocaulis spinksii* Tidwell, Munzing & Banks, *Palaeontographica* 223B:96. 1991.
- Ashicaulis swanensis*** (Tidwell, Munzing & Banks) Tidwell, comb. nov. BASIONYM: *Millerocaulis swanensis* Tidwell, Munzing & Banks, *Palaeontographica* 223B:99. 1991.
- Ashicaulis wadei*** (Tidwell & Rushforth) Tidwell, comb. nov. BASIONYM: *Osmundacaulis wadei* Tidwell & Rushforth, *Bull. Torrey Bot. Club* 97:137. 1970. *Millerocaulis wadei* (Tidwell & Rushforth), Tidwell, *Sida* 11:403. 1987.
- Ashicaulis websterii*** (Tidwell, Munzing & Banks) Tidwell, comb. nov. BASIONYM: *Millerocaulis websterii* Tidwell, Munzing & Banks, *Palaeontographica* 223B: 97. 1991.
- Ashicaulis wrightii*** (Tidwell, Munzing & Banks) Tidwell, comb. nov. BASIONYM: *Millerocaulis wrightii* Tidwell, Munzing & Banks, *Palaeontographica* 223B:93. 1991.

## DISCUSSION

Hill et al. (1989) considered *Australosmunda indentata* the first fossil osmundaceous rhizome described with a simple siphonostele and a parenchymatous pith without realizing that the holotype of *Millerocaulis*, *M. dunlopii*, also has a simple siphonostele. The reason is the considerable confusion surrounding the presence or absence of leaf gaps in *M. dunlopii*. As pointed out by Kidston and Gwynne-Vaughan (1907) in describing the holotype, “The most important anatomical character of this species is the almost complete absence of leaf gaps in the xylem ring of the stem. The fact that most of the leaf traces, *if not all*, depart without in any way interrupting the continuity of the xylem ring, so that the “medullary rays” characteristic of the osmundaceous stele in general are almost or completely absent. Most of these breaks in the xylem ring are clearly



due to accident, but it is just possible that some of them may have been occupied by thin-walled cells which decayed before fossilization. Even if such medullary rays actually were present in the living plant, they must have been extremely narrow and very rare." "... and reference to the longitudinal sections will make it clear that no medullary ray is caused by the departure of the xylem of the leaf-trace and that the continuity of the deeper portion of the xylem ring is undisturbed." (p. 760–761). Thus, this species lacks leaf gaps.

Sinnott (1910), however, attributed the apparent lack of leaf gaps in the holotype of *M. dunlopii* to its having very short and narrow gaps that were obliterated by the process of fossilization, an intriguing explanation but without any real evidence. It is interesting to note that Sinnott also illustrated a diverging leaf trace for *Osmunda regalis* in an "apparently gapless fashion" and one for *O. cinnamomea* and others for *Todea superba* and *T. hymenophylloides* that had not formed complete gaps. The lack of leaf gaps in extant Osmundaceae is rare. Miller (pers. comm. 1993) mentioned that stems of modern osmundaceous taxa may be without complete leaf gaps near branches.

Several osmundaceous specimens with leaf gaps have been reported as *Osmundites* (= *Millerocaulis*) *dunlopii* from the Jurassic of New Zealand (Sinnott 1914) and the Jurassic near Purga, Queensland (Sahni 1920). However, none appear to be that species. One of Sinnott's specimens, for example, is most likely *Ashicaulis wrightii* described from Tasmania (Tidwell et al. 1991). His other specimens also belong to *Ashicaulis* but are too poorly preserved to be identifiable to species. Of the five leaf gaps Sahni (1920) noted in the transverse section of the stem of one of the four incomplete specimens he attributed to *O.* (= *M.*) *dunlopii*, two very narrow gaps may be valid, but even these, could be due to fracturing prior to preservation. None of his alleged gaps have traces opposite them. Sahni further stated, "In the only longitudinal section that was made, three leaf-traces are seen arising, but while it is impossible to say whether all of these have been cut medially, in no case is the cauline strand interrupted opposite an off-coming leaf trace" (p. 13). Furthermore, it is doubtful if the specimen (#140) Sahni (1920) illustrated as text – fig. 2 is *M. dunlopii*, but more likely represents a species of *Ashicaulis*. He founded much of his identification on the curved leaf traces, sclerotic rings, and "the two large sclerotic strands inside the curved ends of the leaf-trace, which is characteristic of *O. dunlopii*." He used these criteria based on the limited knowledge of the Osmundaceae in Australia at the time. It is now known that the first two characters occur in essentially all the extant and extinct species of the Osmundaceae (Hewitson 1962; Miller 1967, 1971) and the last feature in nearly all described species of *Millerocaulis* and *Ashicaulis* from that continent (Tidwell et al. 1991).

The distribution of sclerenchyma in the stipular wings, which has proven to be useful in species determination (Hewitson 1962; Miller 1967), was largely ignored in the specimens reported by Sahni (1920) and Sinnott (1910, 1914) as



*Osmundites* (= *M.*) *dunlopii*. The distribution in the wings of one petiole figured by Sahni (pl. I, fig. 4) was noted to be like that described for *M. dunlopii*, but that particular petiole was not attached to any stem. The stem Sahni (1920) figured (pl. I, fig. 3) had attached petiole bases, but none was figured or described. Consequently, it is doubtful whether any were really *M. dunlopii*.

Edwards (1933) pointed out in discussing his fossil osmundaceous specimen from central Australia that it had a continuous or almost continuous xylem cylinder that was not broken into separate strands similar to the Jurassic species of *Osmundites* (= *Millerocaulis*) *dunlopii*. Medwell (1954), Sharma (1973), and Andrews (1961) all stated or implied that *O.* (= *M.*) *dunlopii* possessed a continuous xylem ring, meaning no leaf gaps.

Miller (1967, 1971) in his papers on the *Osmundaceae* accepted the fossils of Sinnott (1910, 1914) and Sahni (1920) as specimens of *O.* (= *M.*) *dunlopii* and concluded that the species had very narrow, some immediate, some delayed and some incomplete leaf gaps. In addition, he mentioned that the near absence of gaps in the type specimen of this species is not typical for the species. More recently, however, Miller (pers. comm. 1993) commented that in reviewing his notes he had not observed any evidence of leaf gaps when examining slides (#1242–1247) of the holotype of *M. dunlopii* from Gore (Otago), New Zealand at the British Museum of Natural History. He further stated that the holotype of *M. dunlopii* does not have leaf gaps, and that there was never any indication of the short narrow leaf gaps that might have been obliterated in the process of fossilization as per Sinnott's (1910) explanation. Furthermore, Miller noted that Kidston and Gwynne-Vaughan's (1907) photos (pl. I, fig. 3; pl. II, figs. 4–5) do not show any 'obliteration' of the xylem tracheids either. In conclusion, the only definite specimen of *M. dunlopii* known, is its holotype, and it lacks leaf gaps. Consequently, *Australosmunda indentata* is reassigned to *Millerocaulis*. *Millerocaulis dunlopii*, the type, and *M. indica*, which also lacks leaf gaps (Sharma 1973; Fig. 1G), are retained in this genus. Based on photographs of *Osmundacaulis chubutensis* from Argentina (Herbst 1977), this species also appears to be without leaf gaps (Figs. 1H, I, J, K) and is placed in *Millerocaulis* as well.

*Millerocaulis*, as now defined, with a Triassic species (*M. indentata*) and three Jurassic species illustrates another phylogenetic line in the Osmundaceae that is presently known only from the Southern Hemisphere. Osmundaceous taxa of this phylogenetic line in lacking gaps and having parenchymatous piths lend support to the hypothesis that evolution of the parenchymatous pith and evolution of the leaf gap in the xylem cylinder were independent (Hill et al. 1989).

The other species previously assigned to *Millerocaulis* have numerous definite leaf gaps are hereby transferred to the new genus *Ashicaulis*. *Ashicaulis*, presently composed of 22 species, is known from both the Northern and Southern Hemispheres and is currently known from the Triassic to Early Cretaceous.



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